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Genetic Diversity of Two African and Sixteen South American Populations Determined on the Basis of Six Hypervariable Loci

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KEY WORDS DNA polymorphisms; South American blacks; Africans; genetic diversity; VNTR

ABSTRACT A total of 582 individuals (1,164 chromosomes) from two African, eight African-derived South American, five South American Amerindian, and three Brazilian urban populations were studied at four variable number of tandem repeat (VNTR) and two short tandem repeat (STR) hypervariable loci. These two sets of loci did not show distinct allele profiles, which might be expected if different processes promoted their molecular differentiation. The two African groups showed little difference between them, and their intrapopulational variation was similar to those obtained in the African-derived South American communities. The latter showed different degrees of interpopulation variability, despite the fact that they presented almost identical average degrees of non-African admixture. The F_{ST} single locus estimates differed in the five sets of populations, probably due to genetic drift, indicating the need to consider population structure in the evaluation of their total variability. A high interpopulational diversity was found among Amerindian populations in relation to Brazilian African-derived isolated communities. This is probably a consequence of the differences in the patterns of gene flow and genetic drift that each of these semi-isolated groups experienced. Am J Phys Anthropol 109:425–437, 1999.

Wyman and White (1980) were the first to demonstrate that the human genome contains a large number of polymorphic segments which later became known as variable number of tandem repeats (VNTR), since alleles at such loci can be conveniently defined by the number of repeat units of a core sequence. Soon afterwards, Tautz and

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Renz (1984) characterized sequences with a small number of base pairs as repeat units (short tandem repeats; STR). Today, length variations in tandem arrays of sequences ranging from 6–100 base pairs are generally characterized as VNTRs or minisatellites, while the STR or microsatellites present sequences ranging from 2–5 base pairs (Tautz, 1993; Deka et al., 1995; Jin et al., 1996). A large number of such loci have been used to infer human evolutionary history (for recent examples, see Zago et al., 1996; Chakraborty et al., 1997; Jorde et al., 1997; Pérez-Lezaun et al., 1997a,b; Wise et al., 1997).

Recently, the native populations of the Americas have been the focus of intensive genetic studies, based especially on nuclear and mitochondrial DNA (mtDNA) diversity. These studies have provided significant albeit not always concordant information about the origins and history of these populations (Ward et al., 1991; Torroni et al., 1993; Horai et al., 1993; Zago et al., 1995; Santos et al., 1996; Ribeiro dos Santos et al., 1996). The mtDNA of Amerindians has shown at least four lineages of Asian origin, whereas one major and one minor Y-chromosome lineage may have contributed to the peopling of the continent (Rodriguez-Delfin et al., 1997). By contrast, a smaller range of DNA-based genetic studies has been carried out for African Brazilians (Silva and Figueiredo, 1994; Zago et al., 1996; Bortolini et al., 1997a, b, 1998). The data obtained at the protein level and at the nuclear DNA level have contributed to the understanding of the complex evolutionary history of this population that began with the arrival of the first slaves in the first half of the 16th century (Schneider et al., 1987; Bortolini, 1991; Bortolini et al., 1992, 1995, 1997b, 1998).

In the present study, we analyzed the genetic diversity of two African and eight rural African-derived South American populations on the basis of six hypervariable repeat polymorphisms. Additional data for two of these loci were also generated for five South American tribes and for three Brazilian urban populations, complementing earlier studies. Intrapopulation gene diversities (expected heterozygosity) and F-statistics were then estimated. We also calculated the contribution of each locus to the genetic differentiation of these populations.

SUBJECTS AND METHODS

The African samples were obtained from 68 Bantu-speaking subjects, living in two countries: 1) Congo (former Zaire), all samples collected around Lubumbashi City, in Shaba province; and 2) Cameroon, samples collected in Yaoundé City, from Boulou, Bamilake, Bene, Eton, Nweh, Sonaga, and Etongo ethnic groups. The African-derived rural South American samples consisted of 254 individuals from eight communities: 1) Cametá in the region of the lower Tocantins River, State of Pará in northern Brazil; 2) Trombetas, at the margins of the Trombetas and Cumin rivers, state of Pará in northern Brazil; 3) Cajueiro, located in the county of Alcantara, state of Maranhão, in northeastern Brazil; 4) Paredão, in the Porto Alegre metropolitan region, state of Rio Grande do Sul, southern Brazil; 5) Curiepe; 6) Birongo; 7) Sotillo; and (8) Panaquire, all four situated in northern Venezuela, along the north-central coast, in the state of Miranda. The Amerindian samples consisted of 120 individuals from five South American tribes: 1) Arara, who speak a Carib language; 2) Yanomama (isolated language); 3) Wayampi (Tupi); 4) Kayapo (Ge); and 5) Wayana-Apalai (Carib) (data published in Santos et al., 1996). All are located in the Amazonian region. Three Brazilian urban groups were also investigated, and samples were obtained from 140 individuals living in two cities: 1) African-derived people from Ribeirão Preto, located in the north of the state of São Paulo; 2) European-derived individuals from the same city; and 3) Asian-derived (Japanese) subjects from Belém, located in the state of Pará, northern Brazil (Fig. 1). The ethnic classification of the urban samples was made according to physical appearance, and only individuals who reported absence of any other ethnic group in all of the four grandparents were included. Additional information about these populations can be obtained in Schneider et al. (1987), Bortolini (1991), Bortolini et al. (1992, 1994, 1995, 1997a, b, 1998), Santos et al. (1996), and Zago et al. (1996).

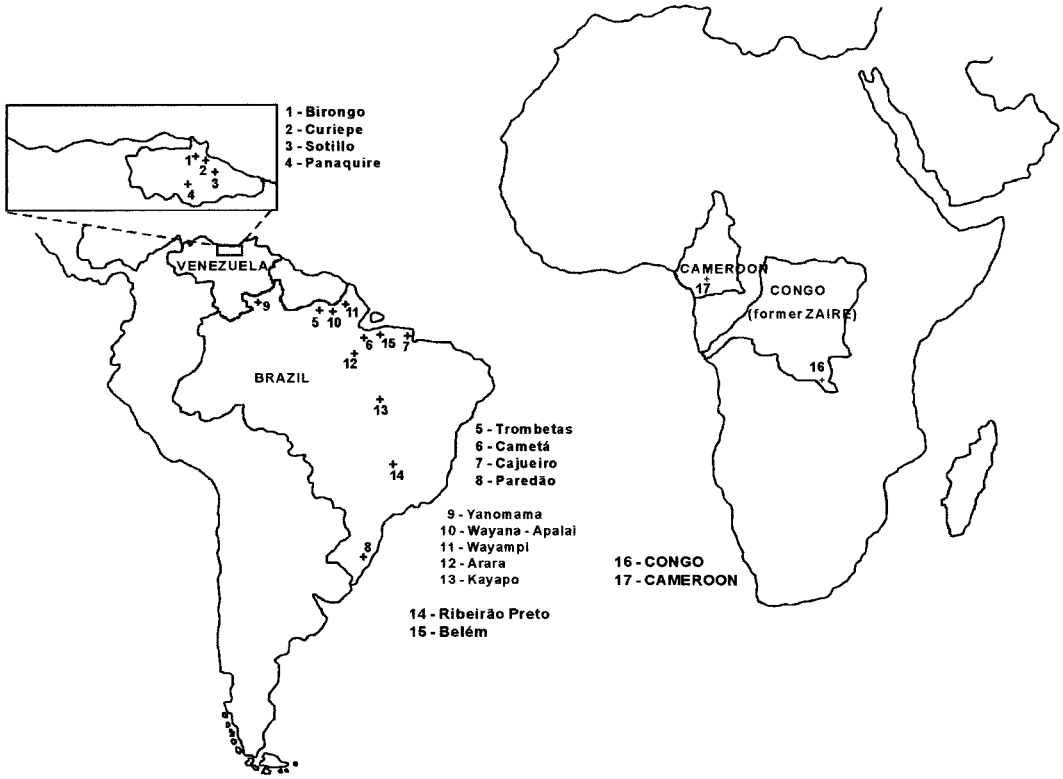

Fig. 1. Geographical location of the populations considered in the present study.

The six hipervariable loci were: 1) D1S80, an extensively investigated polymorphism; 2) APOB, a locus located less than 100 bp 3'of the apoliprotein B gene on chromosome 2; 3) D4S43, which maps to 4p16.3, very close to the locus for Huntington's disease; 4) PAH, which occurs near the 3' region of the gene for phenylalanine-hydroxylase at chromosome 12 (12q24.1); 5) F13A1, located in intron 1 of coagulation factor 13; and 6) vW-I, von Willebrand factor VNTR-I, which occurs within intron 40 of the von Willebrand factor gene. According to the number of tandem repeats, some of these loci were identified as minisatellites (D1S80, APOB, D4S43, and PAH; Goltsov et al., 1992; Horn et al., 1991; Deka et al., 1992, 1994; Hixon et al., 1993), while others were characterized as microsatellites (tetranucleotides; F13A1 and vW-I; Nakamura et al., 1987; Cumming et al., 1992; Wall et al., 1993).

DNA from the Congo, Cameroon, Cajueiro, Ribeirão Preto, Belém, Panaquire, and Amerindian samples were extracted from total blood cells according to the method of Miller et al. (1988). Glycerolized red blood cells that had been frozen at -20°C for about 10 years were used for the DNA extraction from the Paredão, Cametá Trombetas, Curiepe, Birongo, and Sotillo samples, using the phenol/chloroform method (Sambrook et al., 1989). The lengths of repeat unit polymorphisms were analyzed by polymerase chain reaction (PCR) amplification, followed by polyacrylamide gel electrophoresis, the DNA patterns being observed under ultraviolet light after ethidium bromide staining. The primers, reaction times, and electrophoresis conditions for each hypervariable loci considered here were described or referenced in Goltsov et al. (1992), Wall et al. (1993), and Zago et al. (1996). Data on the allele frequencies for four of the hypervariable loci (D1S80, APOB, D4S43, and vW-I) from eight populations (African and European-derived persons from Ribeirão Preto, Asian-derived sub-

jects from Belém, and Amerindian tribes) were obtained from Zago et al. (1996).

Estimates of the intrapopulational gene diversity or expected heterozygosity (H_S) and their standard errors were calculated according to Nei (1987; his equation 8.1), using the DISPAN computer program (Ota, 1993). F-statistics (F_{ST} and F_{IS}) were obtained as described by Weir (1996), using the Genetic Data Analysis Package (Lewis and Zaykin, 1997). F_{IS} is a measure of the amount of nonrandom mating within populations, and in this sense provides an estimate of the inbreeding coefficient in a population; F_{ST} measures the apparent inbreeding in a group of populations that is due to substructuring, and therefore is a measure of population subdivision.

To test if values of F_{IS} or F_{ST} differed significantly from zero, bootstrapping was performed over the loci. In this way, replicate data sets were obtained, for each of which F_{IS} and F_{ST} values were computed. Confidence intervals were defined based on the values obtained in 1,000 replicates which bounded either 95% or 99% of all values (for significance values of 0.05 and 0.01, respectively). If the values in the interval did not include zero, the estimate was considered to be significantly different from zero. The analysis was carried out by the software package of Lewis and Zaykin (1997).

Hierarchical analyses were performed by assigning populations to different "population groups." These groups were analyzed in two ways: 1) they were treated as a single population and comparisons between them were carried out; or 2) F_{ST} was computed at two different hierarchical levels (between populations within a group and between group populations).

Ethnic admixture was calculated using the gene identity method (Chakraborty, 1985), using the ADMIX 3 program, kindly made available to us by Dr. R. Chakraborty. The parental frequencies used for these evaluations were obtained from the following populations included in the appendices: 1) Blacks: Africans from Congo and Cameroon (Appendix A); 2) Amerindians: five populations (Appendix B); and 3) Europeans (Appendix C).

RESULTS

Allele frequency distributions

The average number of alleles per locus was 17.3, with a range from 10 (PAH and vW-I) to 28 (D1S80). The average number of alleles for the Black populations varied in the range of 6.5–10.3 in the rural African-derived populations and 9.5–9.6 in the two African populations, and was 11.0 for the African-derived urban population. The value for the Asian-derived urban population was 8.5, and varied in the 3.2–5.5 range for the five Amerindian tribes. The allele frequencies for each population are listed in Appendices A–C.

Intrapopulational gene diversity and inbreeding

Table 1 shows the intrapopulational gene diversity (H_S) for the 18 populations studied here, considering the six hypervariable loci. The values for the South American rural and urban African-derived populations ranged from 0.77 (Sotillo and Panaquire) to 0.81 (Trombetas and Cametá). These results are similar to those obtained for the Africans investigated here (0.77), and to those estimated in earlier studies, which examined different sets of hypervariable loci for other African populations, including Pygmies (H_S = 0.74–0.81; Bowcock et al., 1994; Deka et al., 1995; Jorde et al., 1995, 1997; Nei and Takezaki, 1996; Pérez-Lezaun et al., 1997b). H_S values observed for the Amerindians ranged from 0.50 (Arara) to 0.70 (Wayana-Apalai and Kayapo), and are similar to those found in other Amerindians (0.52–0.68), with other hypervariable tandem repeat polymorphisms (Bowcock et al., 1994; Deka et al., 1995; Nei and Takezaki, 1996). The H_S observed for the European-derived population of Ribeirão Preto (0.75) is close to the 0.71–0.74 range seen in European Caucasoids (Bowcock et al., 1994; Jorde et al, 1995, 1997; Nei and Takezaki, 1996; Urbanek et al., 1996; Pérez-Lezaun et al., 1997b), while the H_S for the Japanese-derived subjects of Belém (0.66) was almost identical to that obtained for the Japanese in an earlier study (0.67; Nei and Takezaki, 1996).

Table 1 also lists F_{IS} values, which are inbreeding estimators. Interestingly, only

TABLE 1. Average number of alleles for six hypervariable loci and associated F_{IS} (inbreeding coefficient) for 18 human populations

Populations	No. of individuals	Average no. of alleles	H_s[1]	F_{IS}[2]
African				
Congo	34	9.5	0.77 ± 0.04	−0.055
Cameroon	34	9.6	0.77 ± 0.05	0.017
Brazilian, African-derived, rural				
Cametá	40	10.3	0.81 ± 0.02	0.100**
Trombetas	40	9.2	0.81 ± 0.02	0.052*
Cajueiro	44	9.0	0.78 ± 0.03	−0.031
Paredão	20	6.5	0.75 ± 0.05	−0.085
Venezuelan, African-derived, rural				
Curiepe	25	9.5	0.78 ± 0.05	0.091**
Birongo	18	8.2	0.78 ± 0.05	−0.011
Sotillo	33	9.8	0.77 ± 0.05	0.001
Panaquire	34	10.3	0.77 ± 0.05	0.010
South American Indians				
Arara	21	3.2	0.50 ± 0.06	0.049
Wayana-Apalai	25	5.5	0.70 ± 0.05	−0.033
Wayampi	24	3.5	0.56 ± 0.05	−0.097
Yanomama	24	5.0	0.62 ± 0.04	0.041
Kayapo	26	5.5	0.70 ± 0.04	0.012
Brazilian, urban				
European-derived, Ribeirão Preto	50	10	0.75 ± 0.03	0.009
African-derived, Ribeirão Preto	50	11.0	0.79 ± 0.03	−0.019
Asiatic-derived, Belém	40	8.5	0.66 ± 0.07	0.010

[1] Intrapopulation gene diversity (expected heterozygosity).
[2] The inbreeding coefficient for the population.
* $P < 0.05$.
** $P < 0.01$.

TABLE 2. F_{ST} estimates within (diagonal, underlined) and between population sets[1]

Population groups	1	2	3	4	5
African (1)	0.002				
Brazilian, African-derived (2)	0.026**	0.013*			
Venezuelan, African-derived (3)	0.015**	0.015**	0.014		
South American Indians (4)	0.128*	0.055*	0.102*	0.112**	
Brazilian, urban (5)	0.032*	0.007	0.013	0.067**	0.105*

[1] 1, Congo and Cameroon; 2, Cametá Trombetas, Cajueiro, and Paredão; 3, Curiepe, Birongo, Sotillo, and Panaquire; 4, Arara, Wayana-Apalai, Wayampi, Yanomam, and Kayapo; 5, African-derived, Ribeirão Preto, European-derived, Ribeirão Preto, and Asiatic-derived, Belém. The F_{ST} obtained, considering the 18 populations, was 0.085.**
* $P < 0.05$.
** $P < 0.01$.

three African-derived populations presented a significant level of inbreeding: Cametá, Trombetas, and Curiepe. This finding reflects the effects of characteristics which are restricted to these three populations, such as sex differences in gamete frequencies, assortive mating, sample size, migration, and mixtures of subdivisions (Long, 1986).

Differentiation within and between sets of populations

Table 2 presents the differentiation within and between groups of populations. The F_{ST} value for the group consisting of the four rural African-derived Brazilian populations is 0.013. This number is significantly different from zero ($P < 0.01$), and can be interpreted in two ways: 1) the populations diverged in Brazil, after their arrival; or 2) these populations were founded by Africans or descendants of African populations which were significantly different from each other in Africa. It is difficult to distinguish between these alternatives because both generate similar patterns of variation, and it is possible that both effects are relevant. The eight rural African-derived populations studied here have small effective population sizes, present different levels of interethnic admixture, and have probably experienced

TABLE 3. F_{ST} single-locus estimates, considering five groups of populations and a group comprising all populations[1]

	Population sets					
Loci	African (N = 2; n = 68)[1]	Brazilian, African-derived, rural (N = 4; n = 144)	Venezuelan, African-derived, rural (N = 4; n = 110)	South American Indians (N = 5; n = 120)	Brazilian, urban (Ribeirão Preto and Belém) (N = 3; n = 140)	All (N = 18; n = 582)
D1S80	0.017	0.018	0.007	0.087	0.017	0.064
APOB	0.001	0.024	−0.003	0.137	0.096	0.083
D4S43	−0.004	0.005	0.067	0.080	0.109	0.135
PAH	0.007	0.004	0.028	0.112	0.216	0.109
F13A1	−0.008	0.014	0.004	0.110	0.110	0.069
vW-I	−0.004	0.009	−0.007	0.145	0.088	0.055
All loci	0.002	0.013*	0.014	0.112**	0.105*	0.085**

[1] N, number of populations; n, number of individuals.
* $P < 0.05$.
** $P < 0.01$.

bottlenecks in the past (Bortolini et al., 1992, 1995). Note, however, that the F_{ST} result considering the four Venezuelan populations (0.014) is not significantly different from zero. This may be due to the fact that they are relatively close geographically (see Fig. 1).

The high level of differentiation between the five Amerindian populations (F_{ST} = 0.112) was expected. Several earlier studies with different genetic markers (classical protein polymorphisms, and mitochondrial and nuclear DNAs) revealed a similar situation, with the Amerindian populations presenting a higher genetic heterogeneity than any other major human ethnic group (Cavalli-Sforza et al., 1994; Bortolini et al., 1997b,c; Deka et al., 1995; Bortolini and Salzano, 1996; Urbanek et al., 1996; Zago et al., 1996). Some peculiarities, such as population structure, bottleneck effects, tribal isolation, and depopulation due to contact with European colonizers, have been identified as probable causes for this phenomenon.

The F_{ST} value obtained for the urban Brazilians (0.105), which is significantly different from zero ($P < 0.05$), was expected because these populations are representative of the three major ethnic groups (African, European, and Asian).

The two African populations did not show significant gene differentiation. This result reflects the biological unity of the Bantu-speaking peoples, probably due to their recent and massive expansion (Cavalli-Sforza et al., 1994). However, when the Africans are compared with the two African-derived rural groups of populations, the F_{ST} values obtained (0.026 and 0.015) were significantly different from zero ($P < 0.01$). There is no doubt that Bantu groups contributed to African-South American populations, but it is not clear how much the allele frequencies of the African populations investigated here are similar to those of the parental African groups. Furthermore, earlier investigations using other genetic markers with the same African-derived samples revealed that they present different degrees of interethnic exchange (Bortolini et al., 1995), and this could also have contributed to the heterogeneity found.

The average F_{ST} value for the six VNTR/STR loci, considering the 18 populations investigated here, was 0.085 (Table 2), which is significantly different from zero ($P < 0.05$). This value is identical to that obtained by Pérez-Lezaun et al. (1997b), who tested 20 microsatellite loci with a 4–6-bp repeat unit in 16 worldwide human populations. Note, however, that this number is somewhat lower than the global estimates of gene differentiation obtained using classical markers (F_{ST} = 0.119: Cavalli-Sforza et al., 1994; G_{ST} = 0.168: Livshits and Nei, 1990), restriction fragment length polymorphisms (F_{ST} = 0.139: Cavalli-Sforza et al., 1994), or mtDNA (G_{ST} = 0.199: Jorde et al., 1995).

Within- and between-locus differences

Table 3 summarizes the information about the F_{ST} single-locus estimates. Values ranged from 0.055–0.135; the Fst values corresponded to the amount of variation between populations. This means that the amount of variation within populations ranged from

0.95–0.87 (where within-population contributions to total variance are approximately 1- F_{ST}). This is a consequence of their differences in history and population structure, where genetic drift has a fundamental role in the generation of the genetic differences of the populations (Nei, 1987).

Variation in F_{ST} values across markers is an expected behavior, and explains why studies aiming to reconstruct population histories must rely on a large number of markers (Long, 1986).

Interethnic admixture

Considering the two sets of populations as a whole, we obtain almost identical average degrees of admixture, as estimated by the VNTR/STR markers (Brazilian African-derived groups: 52 ± 4%, 36 ± 3%, and 12 ± 2% of African, European, and Amerindian genes, respectively; Venezuelan African-derived communities: 52 ± 5%, 37 ± 4%, and 11 ± 3% of African, European, and Amerindian genes, respectively). The substantial non-African ancestry estimated by these values indicates that admixture with subjects of other ethnic extractions has been extensive. In addition, these data also reveal that the percentage of African genes ranges from 52% to 70% in isolates and selected urban Blacks, respectively.

DISCUSSION

The intrapopulational gene diversities observed in African-derived South American populations reveal similarity with those obtained from Africans. Lower levels of gene diversity could be expected among the South American populations, since just a subsample of Africans was brought to South America as slaves (Africa had about 100 million inhabitants at the time of slavery; Curtin et al., 1991). Additionally, the rural populations considered here have small effective sizes and probably experienced bottlenecks in the past. A possible explanation for this similarity is that the hypervariable loci would have restored intrapopulational gene diversity, through mutations, after the population bottleneck (Menotti-Raymond and O'Brian, 1993; Clark et al., 1995); despite the high mutation rate for microsatellites, the short period since migration from Africa seem insufficient to account for that. A more plausible explanation is that the similar diversity levels between African and African-derived populations resulted from the interethnic admixture which occurred in South America. There are several suggestions that admixed populations may show higher expected heterozygosities when compared to those of the source populations from which they were derived (Byard et al., 1985), although this notion is not universally accepted (Chakraborty, 1986).

One of the questions in which we are interested concerns the relationship between South American populations of African ancestry and extant African populations. In order to perform such an analysis it is necessary to obtain data on the African populations which are the putative ancestors of the Brazilian populations. Here we present results obtained with two African populations which are not believed to be those from which Brazilian populations were founded. However, this comparison allows us to examine how the differentiation between populations of Zaire and Cameroon compares to that between South American populations. When African and African-derived Brazilians are compared, an F_{ST} of 0.026 is obtained, which is significant ($P < 0.01$) (Table 2). When Venezuelans, African-derived, and Africans are compared, an F_{ST} of 0.015 is obtained, which is also significantly different from zero ($P < 0.01$).

Some investigations have shown that the VNTR/STR loci present unequal mutation rates among alleles as well as a limited range of allele sizes (Jeffreys et al., 1988; Devlin and Risch, 1992; Garza et al., 1995). Our results concerning the F_{ST} single-locus analysis, however, reveal in addition that this diversity measure is not uniform among the population sets. Sampling problems and other causes, especially genetic drift, may be responsible for this heterogeneity. However, a complex combination of intrinsic and extrinsic factors probably determines the final population variability observed at these loci.

It is interesting to compare the values obtained for the present set of markers and populations with those obtained from other studies and for non-African populations. The mean heterozygosity observed for the VNTRs

is 0.78 for all South American populations of African ancestry, a value which is similar to that obtained using 30 microsatellite markers (0.81) for a set of African populations. Weir (1996) examined data for ethnic groups sampled within the United States, and the results indicated a very low differentiation between African populations in the US sampled from three localities: Florida, Texas, and California, with the estimates of F_{ST} ranging from 0.002–0.001. This may be a consequence of the Brazilian populations having been sampled from isolates, whereas the US samples were collected from blood banks.

Genetic diversity of Black populations is lower than the genetic diversity of Amerindians. This finding can be explained by three factors: 1) The degree of admixture with Caucasians and Amerindians (36% and 12%, respectively) shows that the "isolation" of Black isolates is only partial. Consequently, the diversity lost by genetic drift, during isolation process, was reintroduced by admixture with other racial groups; 2) The Amerindian subpopulations (tribes) are much more isolated, and many are quite small (less than 1,000 individuals), favoring genetic drift. However, we have demonstrated genetic flow between tribes of different language groups (Zago et al., 1995; Santos et al., 1996); and (3) The evolution time of Amerindian populations (20,000 years) in America is much longer than that of Black populations (400 years).

In summary, the Black and Amerindian populations of Brazil follow completely different evolutionary histories. While Black populations show a pattern of homogeneity and evolving admixture with whites over a relatively short period of 400 years, the Amerindians are characterized by small, isolated, heterogeneous populations, which have been developing for many thousands of years.

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APPENDIX A. Allele frequencies for the six hypervariable loci in two African and eight African-derived rural South American populations[1]

		Populations									
Locus	Alleles	Congo	Cameroon	Cametá	Trombetas	Cajueiro	Paredão	Curiepe	Sotillo	Panaquire	Birongo
D1S80	16	0.018									
	17	0.036	0.029	0.038	0.025		0.026	0.020	0.016		
	18	0.036	0.015	0.150	0.175	0.318	0.264	0.120	0.172	0.191	0.118
	20		0.059	0.038						0.118	
	21	0.274	0.132	0.087	0.150	0.155	0.158	0.060	0.109	0.044	0.147
	22	0.164	0.059	0.112	0.037		0.131	0.100	0.031	0.015	0.118
	23	0.018	0.044	0.050	0.025		0.026	0.020	0.016	0.044	0.029
	24	0.146	0.177	0.213	0.263	0.131	0.211	0.300	0.249	0.191	0.118
	25	0.036	0.073	0.075	0.037	0.059		0.100	0.047	0.073	0.206
	26	0.018	0.015		0.012			0.020		0.015	
	27	0.036	0.029			0.036		0.020	0.016	0.015	
	28	0.018	0.162	0.062	0.062	0.131	0.026	0.120	0.094	0.147	0.118
	29	0.018		0.038	0.050			0.040	0.016	0.015	0.029
	30			0.050	0.025				0.062		0.088
	31	0.018		0.038	0.075	0.012			0.062	0.029	
	32			0.012		0.059			0.031		0.029
	34	0.164	0.191	0.025	0.052	0.036	0.105	0.060	0.047	0.103	
	35		0.015								
	37								0.016		
	38								0.016		
	39				0.012		0.053				
	42			0.012							
	45							0.020			
	n	34	34	40	40	44	16	25	32	34	17

APPENDIX A. (continued)

		Populations									
Locus	Alleles	Congo	Cameroon	Cametá	Trombetas	Cajueiro	Paredão	Curiepe	Sotillo	Panaquire	Birongo
APOB	20			0.013							
	21	0.015	0.015			0.011		0.043	0.015		
	24	0.029	0.015	0.013							
	25	0.015				0.046					
	26							0.022			
	28		0.029		0.013	0.011		0.043	0.015	0.015	0.055
	29	0.029	0.029	0.013		0.023		0.022	0.030	0.015	
	30	0.073	0.059	0.025	0.050	0.102		0.022	0.030	0.088	0.111
	31			0.037							
	32	0.044	0.029	0.062	0.013			0.087	0.091	0.103	0.028
	33		0.015								
	34	0.103	0.161	0.138	0.162	0.170	0.225	0.197	0.258	0.235	0.280
	36	0.207	0.118	0.238	0.262	0.182	0.425	0.087	0.212	0.191	0.222
	37	0.015									
	38	0.044	0.073	0.037	0.025	0.046		0.022	0.045	0.015	
	40	0.059	0.044	0.037	0.013	0.057	0.075	0.065	0.061	0.059	0.055
	42	0.176	0.103	0.138	0.050	0.011		0.043	0.061	0.059	0.055
	44	0.088	0.118	0.100	0.225	0.023	0.100	0.152	0.061	0.029	0.028
	46	0.059	0.103	0.112	0.125	0.068	0.150	0.130	0.091	0.073	0.055
	47		0.015			0.102	0.025				
	48		0.059	0.037	0.062	0.046		0.065	0.030	0.059	0.083
	50	0.029				0.102				0.044	
	52		0.015								
	56	0.015								0.015	
	n	34	34	40	40	44	20	23	33	34	18
D4S43	1	0.545	0.617	0.256	0.238	0.319	0.275	0.562	0.652	0.637	0.677
	2	0.250	0.249	0.320	0.351	0.274	0.350	0.292	0.015	0.015	
	3	0.029		0.013		0.102	0.025			0.030	0.028
	4					0.011					
	5							0.021			
	6	0.147	0.074	0.077	0.113	0.068	0.025	0.062	0.076		0.055
	7		0.015	0.167	0.050	0.079	0.175	0.042	0.182	0.182	0.111
	8		0.015								
	9								0.015		
	10			0.026	0.025	0.023	0.100	0.021	0.015		
	11	0.029	0.015	0.090	0.187	0.079	0.050		0.045	0.091	0.139
	12		0.015	0.026	0.012	0.011				0.030	
	13			0.013	0.012					0.015	
	14				0.012						
	16			0.013							
	17					0.034					
	n	34	34	40	40	44	20	25	33	33	18
PAH	3			0.128	0.125	0.136	0.075	0.042	0.091	0.059	0.167
	4									0.015	0.028
	7	0.016		0.103	0.025		0.125	0.104	0.091	0.044	0.055
	8	0.117	0.309	0.282	0.263	0.352	0.225	0.416	0.182	0.206	0.307
	9	0.420	0.470	0.332	0.412	0.330	0.375	0.271	0.485	0.515	0.250
	10	0.177	0.118	0.090	0.050	0.057	0.200	0.083	0.106	0.088	0.055
	11	0.065	0.029	0.026	0.025	0.034		0.021			
	12	0.145	0.059	0.026	0.025	0.068		0.042	0.015	0.044	0.055
	13		0.015		0.075	0.023		0.021	0.030	0.029	0.083
	14			0.013							
	n	31	34	39	40	40	20	24	33	34	18
F13A1	1	0.034	0.030	0.112	0.162	0.102	0.030	0.060	0.076	0.029	0.055
	2	0.191	0.152	0.263	0.162	0.227	0.235	0.160	0.182	0.265	0.305
	3	0.465	0.409	0.301	0.263	0.296	0.235	0.200	0.304	0.250	0.250
	4							0.020			
	5	0.070	0.076	0.087	0.126	0.296	0.235	0.100	0.121	0.162	0.139
	6	0.086	0.121	0.188	0.200	0.045	0.235	0.300	0.212	0.074	0.167
	8	0.103	0.106	0.025	0.037	0.034	0.030	0.060	0.015	0.074	0.028
	12	0.017								0.029	
	13	0.017	0.030		0.025			0.040	0.045	0.059	0.028
	14								0.015	0.029	
	15	0.017	0.076	0.012	0.025			0.020	0.030	0.029	
	16			0.012				0.040			0.028
	n	29	33	40	40	44	17	25	33	34	18

(*Continued*)

APPENDIX A. (continued)

Locus	Alleles	Populations									
		Congo	Cameroon	Cametá	Trombetas	Cajueiro	Paredão	Curiepe	Sotillo	Panaquire	Birongo
vW-I	5	0.206	0.220	0.162	0.200	0.244	0.250	0.220	0.228	0.192	0.222
	6	0.397	0.294	0.437	0.363	0.342	0.300	0.460	0.410	0.427	0.361
	7	0.132	0.147	0.050	0.075	0.134	0.200	0.040	0.121	0.029	0.111
	8	0.015	0.015	0.013					0.030	0.015	
	9	0.118	0.118	0.050	0.087	0.146	0.025	0.120	0.015	0.088	0.139
	10	0.103	0.074	0.175	0.125	0.085	0.075	0.080	0.106	0.103	0.139
	11	0.029	0.132	0.113	0.150	0.012	0.150	0.080	0.060	0.088	0.028
	12					0.037			0.030	0.029	
	13									0.029	
	n	34	34	40	40	41	20	25	33	34	18

[1] n, number of individuals.

APPENDIX B. Allele frequencies for the six hypervariable loci in five South American Indian groups[1]

Locus	Alleles	Populations				
		Arara	Wayampi	Yanomama	Kayapo	Wayana-Apalai
D1S80	18	0.333	0.560	0.460	0.320	0.320
	21					0.020
	23	0.143			0.020	0.020
	24			0.160	0.160	0.040
	25		0.040	0.180	0.120	0.260
	26				0.040	0.020
	28				0.160	0.040
	29			0.060		0.020
	30	0.520	0.400	0.020	0.100	0.260
	31				0.060	0.080
	33				0.020	
	46				0.040	
	n	21	25	25	26	26
APOB	30			0.100	0.038	
	34	0.143	0.042		0.096	0.040
	36	0.690	0.208	0.520	0.327	0.640
	38			0.040	0.019	
	44			0.060	0.173	
	46	0.167	0.750	0.260	0.327	0.320
	48			0.020	0.019	
	n	21	25	25	26	26
D4S43	1	0.780	0.438	0.625	0.442	0.560
	4				0.019	
	7		0.208	0.063	0.308	0.160
	10		0.042		0.019	0.020
	11	0.214	0.020	0.292	0.212	0.200
	14					0.040
	16		0.292			
	17			0.021		0.020
	n	21	25	25	26	26
PAH	3	0.381	0.077	0.042	0.135	0.340
	8	0.309	0.385	0.104	0.038	0.100
	9	0.167	0.538	0.167	0.154	0.240
	10	0.143		0.687	0.673	0.320
	n	21	26	24	26	25
F13A1	1	0.143	0.269	0.100	0.300	0.120
	2	0.762	0.192	0.360	0.440	0.280
	3	0.095	0.385	0.160	0.220	0.260
	5		0.154	0.020	0.020	0.180
	6			0.360	0.020	0.160
	n	21	26	25	25	25
vW-I	5		0.152			
	6	0.667	0.717	0.500	0.269	0.327
	8					0.038
	9			0.180	0.096	0.115
	10	0.024		0.320	0.385	0.346
	11		0.130		0.250	0.135
	12	0.309				0.038
	n	21	25	25	26	26

[1] The data related to D1S80, APO-B, D4S43, and vWF-I were reported in Zago et al. (1996), and are reproduced here to provide the whole set in a single place. n, number of individuals.

APPENDIX C. Allele frequencies for six hypervariable loci in three Brazilian urban groups[1]

Locus	Alleles	Populations: African-derived Ribeirão Preto	European-derived Ribeirão Preto	Asiatic-derived Belém
D1S80	16		0.020	0.013
	17	0.020		
	18	0.060	0.190	0.141
	19		0.010	0.026
	20	0.020	0.060	
	21	0.100	0.020	0.026
	22	0.050	0.050	0.013
	23	0.030		
	24	0.260	0.350	0.281
	25	0.060	0.050	0.013
	26		0.030	0.013
	27	0.060		0.026
	28	0.160	0.080	0.114
	29	0.030	0.060	0.013
	30	0.020		0.051
	31	0.010	0.050	0.166
	32	0.030		0.013
	33		0.010	
	34	0.090	0.020	0.013
	36			0.013
	37			0.026
	38			0.013
	39			0.013
	41			0.013
	n	50	50	39
APO-B	21	0.010		
	24	0.010		
	25	0.010		
	30	0.050	0.070	0.037
	31	0.010		
	32	0.030	0.090	0.162
	34	0.140	0.170	0.574
	36	0.280	0.400	0.150
	38	0.060	0.070	0.013
	39	0.010		
	40	0.090	0.030	
	42	0.180	0.010	
	44	0.050	0.030	
	46	0.030	0.040	0.025
	48	0.040	0.090	0.013
	54			0.013
	64			0.013
	n	50	50	40
D4S43	1	0.500	0.133	0.269
	2	0.230	0.071	0.371
	3	0.030		
	6	0.080	0.051	
	7	0.070	0.409	0.154
	8	0.010		
	9	0.010	0.051	0.013
	10	0.030	0.082	0.013
	11	0.040	0.143	0.167
	12		0.020	0.013
	13		0.020	
	14		0.010	
	17		0.010	
	n	50	49	39
PAH	3	0.060	0.378	0.800
	7	0.030	0.112	0.025
	8	0.260	0.387	0.175
	9	0.300	0.092	
	10	0.070		
	11	0.040		
	12	0.080	0.031	
	13	0.060		
	n	50	49	40
F13A1	1	0.100	0.041	0.128
	2	0.070	0.071	0.282
	3	0.320	0.205	0.038
	4		0.020	
	5	0.110	0.276	0.539
	6	0.180	0.306	0.013
	8	0.070		
	11		0.010	
	12	0.030	0.020	
	13	0.030		
	14	0.020	0.010	
	15	0.030	0.031	
	16	0.010	0.010	
	n	50	49	30
vW-I	1		0.010	
	5	0.180	0.100	0.012
	6	0.450	0.570	0.187
	7	0.070	0.030	
	8	0.020	0.020	
	9	0.080	0.060	0.327
	10	0.140	0.100	0.287
	11	0.060	0.100	0.175
	12		0.010	0.012
	n	50	50	40

[1] n, number of individuals.

LITERATURE CITED

Bortolini MC. 1991. Estudos genéticos em comunidades Negras Isoladas Sul-Americanas. M.Sc. thesis, Curso de Pós-Graduação em Genética e Biologia Molecular. Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

Bortolini MC, Salzano FM. 1996. mtDNA diversity analysis in Amerindians and other human populations—"how different are they? Braz J Genet 19:527–534.

Bortolini MC, Weimer TA, Franco MHLP, Salzano FM, Layrisse Z, Schneider H, Schneider MP, Harada ML. 1992. Genetic studies in three South American Black populations. Gene Geogr 6:1–6.

Bortolini MC, Weimer TA, Franco MHLP, Salzano FM, Callegari-Jacques SM, Schneider H, Layrisse Z. 1994. The ethnic origin of South American Blacks: an estimate using genetic data. Anthropol Biol 2:53–62.

Bortolini MC, Weimer TA, Salzano FM, Callegari-Jacques SM, Schneider H, Layrisse Z, Bonatto SL. 1995. Evolutionary relationships between Black South American and African populations. Hum Biol 67:547–559.

Bortolini MC, Zago MA, Salzano FM, Silva WA Jr, Bonatto SL, Da Silva MCBO, Weimer TA. 1997a. Evolutionary and anthropological implications of mitochondrial DNA variation in African-Brazilian populations. Hum Biol 69:141–159.

Bortolini MC, Salzano FM, Zago MA, Silva WA Jr, Weimer TA. 1997b. Genetic variability in two Brazilian ethnic groups: a comparison of mitochondrial and protein data. Am J Phys Anthropol 103:147–156.

Bortolini MC, Weimer TA, Salzano FM, Moura LB. 1997c. Genetic structure of two urban Afro-Brazilian populations. Int J Anthropol 12:5–16.

Bortolini MC, Silva WA Jr, Weimer TA, Zago MA, Castro de Guerra D, Shneider MP, Layrisse Z, Mendez Castellano H, Salzano FM. 1998. Protein and hypervariable tandem repeat diversity in eight African-derived South-American populations: inferred relationships do not coincide. Hum Biol 70:443–461.

Bowcock AM, Ruiz-Linares A, Tomfohrde J, Minch E, Kidd JR, Cavalli-Sforza LL. 1994. High resolution of human evolutionary trees with polymorphic microsatellites. Nature 368:455–457.

Byard PJ, Schanfield MS, Crawford MH. 1985. Admixture and heterozygosity in West Alaskan populations. J Biosoc Sci 15:207–216.

Cavalli-Sforza LL, Menozzi P, Piazza A. 1994. History and geography of human genes. Princeton: Princeton University Press. 413 p.

Chakraborty R. 1985. Gene identity in racial hybrid and estimation of admixture rates. In: Ahuja YR, Neel JV, editors. Genetic differentiation in human and other animal populations. Delhi: Indian Anthropological Association. p 1771–1780.

Chakraborty R. 1986. Gene admixture in human populations: models and predictions. Yrbk Phys Anthropol 29:1–43.

Chakraborty R, Kimmel M, Stivers DN, Davison LJ, Deka R. 1997. Relative mutation rates at di-, tri-, and tetranucleotide microsatellite loci. Proc Natl Acad Sci USA 94:1041–1046.

Clark AG, Hamilton JF, Chambers GK. 1995. Inference of population subdivision from VNTR distributions of New Zealanders. Genetica 96:37–49.

Cumming AM, Amstrong JG, Pendry K, Burn AM, Wensley RT. 1992. Polymerase chain reaction amplification of two polymorphic simple repeat sequences within the von Willebrand factor gene: application to family studies in von Willebrand disease. Hum Genet 89:194–198.

Curtin P, Feierman S, Thompson L, Vansina J. 1991. African history. New York: Longman. 338 p.

Deka R, Chakraborty R, DeCroo S, Rothhammer F, Barton AS, Ferrell RR. 1992. Characteristics of polymorphisms at a VNTR locus 3' to the apolipoprotein B gene in five human populations. Am J Hum Genet 51:1325–1333.

Deka R, DeCroo S, Jin L, McGarvey ST, Rothhammer F, Ferrell RE, Chakraborty R. 1994. Population genetic characteristics of the D1S80 locus in seven human populations. Hum Genet 94:252–258.

Deka R, Shriver MD, Yu LM, Ferrel RE, Chakraborty R. 1995. Intra and inter-population diversity at short tandem repeat loci in diverse populations of the world. Electrophoresis 16:1659–1664.

Devlin B, Risch N. 1992. A note on Hardy-Weinberg equilibrium of VNTR data by using the Federal Bureau of Investigation's fixed-bin method. Am J Hum Genet 51:549–553.

Garza JC, Slatkin M, Freimer NB. 1995. Microsatellite allele frequencies in humans and chimpanzees, with implications for constraints on allele size. Mol Biol Evol 12:594–603.

Goltsov AA, Eisensmith RC, Konecki DS, Lichter-Konecki U, Woo SLC. 1992. Associations between mutations and a VNTR in the human phenylalanine hydroxylase gene. Am J Hum Genet 51:627–636.

Hixon JE, Powers PK, McMahan CA. 1993. The human apolipoprotein B 3' hypervariable region: detection of eight new alleles and comparison of allele frequencies in Blacks and Whites. Hum Genet 91:475–479.

Horai S, Kondo R, Nakagawa-Hattori Y, Hayashi S, Sonoda S, Tajima K. 1993. Peopling of the Americas founded by four major lineages of mitochondrial DNA. Mol Biol Evol 10:23–47.

Horn GT, McClatchey AI, Richards B, MacDonald ME, Gusella JF. 1991. Detection by PCR of a VNTR polymorphism at D4S43. Nucleic Acids Res 19:4772.

Jeffreys AJ, Royle NJ, Wilson V, Wong Z. 1988. Spontaneous mutation rates to new length alleles at tandem-repetitive loci in human DNA. Nature 332:278–281.

Jin L, Macaubas C, Hallmayer J, Kimura A, Mignot E. 1996. Mutation rate varies among alleles at a microsatellite locus: phylogenetic evidence. Proc Natl Acad Sci USA 93:15285–15288.

Jorde LB, Bamshad MJ, Watkins WS, Zenger R, Fraley AE, Krakowiak PA, Carpenter KD, Soodyal H, Jenkins T, Rogers AR. 1995. Origins and affinities of modern humans: a comparison of mitochondrial and nuclear genetic data. Am J Hum Genet 57:523–538.

Jorde LB, Rogers AR, Bamshad MJ, Watkins WS, Krakowiak P, Sung S, Kere J, Harpending HC. 1997. Microsatellite diversity and the demographic history of modern humans. Proc Natl Acad Sci USA 94:3100–3103.

Lewis PO, Zaykin D. 1997. Genetic data analysis: computer program for the analysis of allelic data. Version 1.0. Internet, Genetic Data Analysis home page: http://chee.unm.edu/gda/

Livshits G, Nei M. 1990. Relationships between intrapopulational and interpopulational genetic diversity in man. Ann Hum Biol 6:501–503.

Long JC. 1986. The allelic correlation structure of Gainj-and Kalam-speaking people. I. The estimation and interpretation of Wright's F-statistics. Genetics 112: 629–647.

Menotti-Raymond M, O'Brian S. 1993. Dating the genetic bottleneck of the African cheetah. Proc Natl Acad Sci USA 90:3172–3176.

Miller SA, Dykes DD, Polesky F. 1988. A simple salting-out procedure for extracting DNA from human nucleated cells. Nucleic Acids Res 16:1215.

Nakamura Y, Leppert M, O'Connell M, Wolff R, Holm T, Culver M, Martin C, Fujimoto E, Hoff M, Kumlin W, White R. 1987. Variable number of tandem repeat (VNTR) markers for human gene mapping. Science 235:1616–1622.

Nei M. 1987. Molecular evolutionary genetics. New York: Columbia University Press. 512 p.

Nei M, Takezaki N. 1996. The root of the phylogenetic tree of human populations. Mol Biol Evol 13:170–177.

Ota T. 1993. DISPAN: genetic and phylogenetic analysis. University Park, PA: Institute of Molecular Evolutionary Genetics, Pennsylvania State University.

Pérez-Lezaun A, Calafell F, Mateu E, Coma D, Bosh E, Bertranpetit J. 1997a. Allele frequencies for 20 microsatellites in a worldwide population survey. Hum Hered 47:189–196.

Pérez-Lezaun A, Calafell F, Mateu E, Coma D, Ruiz-Pacheco R, Bertranpetit J. 1997b. Microsatellite variation and the differentiation of modern humans. Hum Genet 99:1–7.

Ribeiro dos Santos AK, Santos SE, Machado AL, Guapindaia V, Zago MA. 1996. Heterogeneity of mitochondrial DNA haplotypes in pre-Colombian natives of the Amazon region. Am J Phys Anthropol 101:29–37.

Rodriguez-Delfin L, Santos SE, Zago MA. 1997. Diversity of the human Y chromosome of South American Amerindians: a comparison with Blacks, Whites, and Japanese from Brazil. Ann Hum Genet 61:439–444.

Sambrook J, Fritsch EF, Maniatis T. 1989. Molecular cloning: a laboratory manual, 2nd ed. Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.

Santos SEB, Ribeiro-dos-Santos AKC, Meyer D, Zago MA. 1996. Multiple founder haplotypes of mitochondrial DNA in Amerindians revealed by RFLP and sequencing. Ann Hum Genet 60:305–319.

Schneider H, Guerreiro JF, Santos SEB, Weimer TA, Schneider MP, Salzano FM. 1987. Isolate breakdown in Amazonia. The Blacks of the Trombetas River. Braz J Genet 10:565–574.

Silva WA Jr, Figueiredo MS. 1994. Analysis of factor VIII gene polymorphisms in Brazilian Blacks reveals further differences in the Black population. Hum Hered 44:252–260.

Tautz D. 1993. Notes on the definition and nomenclature of tandemly repetitive DNA sequences. In: Pena SDJ, Chakraborty R, Epplen JT, Jeffreys J, editors. DNA fingerprinting: state of the science. Basel: Birkuser Verlag. p 21–28.

Tautz D, Renz M. 1984. Single sequences are ubiquitous repetitive components of eukaryotic genomes. Nucleic Acids Res12:4127–4138.

Torroni A, Schurr TG, Cabell MF, Brown MD, Neel JV, Larsen M, Smith DG, Vullo CM, Wallace DC. 1993. Asian affinities and continental radiation of the four founding Native American mtDNA. Am J Hum Genet 53:563–590.

Urbanek M, Goldman D, Long JC. 1996. The apportionment of dinucleotide repeat diversity in Native Americans and Europeans: a new approach to measuring gene identity reveals asymmetric patterns of divergence. Mol Biol Evol 13:943–953.

Wall WJ, Williamson R, Petrou M, Papaioannou D, Parkin BH. 1993. Variation of short tandem repeats within and between populations. Hum Mol Genet 2:1023–1029.

Ward RH, Frazier BL, Dew-Jager K, Pääbo S. 1991. Extensive mitochondrial diversity within a single Amerindian tribe. Proc Natl Acad Sci USA 90:10663–10667.

Weir BS. 1996. Genetic data analysis II—"methods for discrete population genetic data, 2nd ed. Sunderland: Sinauer.

Wise CA, Sraml M, Rubinsztein DC, Easteal S. 1997. Comparative nuclear and mitochondrial genome diversity in humans and chimpanzees. Mol Biol Evol 14:707–716.

Wyman AR, White R. 1980. A highly polymorphic locus in human DNA. Proc Natl Acad Sci USA 77:6754–6758.

Zago MA, Melo-Santos, EJ, Clegg JB, Guerreiro JF, Martinson JJ, Norwich J, Figueiredo MS. 1995. α-globin gene haplotypes in South American Indians. Hum Biol 67:535–545.

Zago MA, Silva WA Jr, Tavella MH, Santos SEB, Guerreiro JF, Figueiredo MS. 1996. Interpopulational and intrapopulational genetic diversity of Amerindians as revealed by six variable number of tandem repeats. Hum Hered 46:274–289.